

Alberto Mattavelli & Giacomo Bracchi

Palaeoenoploides alessandrellianus n. gen. n. sp.:
a Late Cenomanian 'roundworm' from the
Upper Cretaceous of Lebanon (Nematoda: Enoplidae)

Abstract - The Late Cenomanian nematode *Palaeoenoploides alessandrellianus* n. gen. n. sp. from the sub-lithographic limestones of Haqel (Lebanon) is herein described on the basis of 172 studied specimens. The architecture of the teeth of a fossil nematode is illustrated for the first time. Exceptionally, some specimens preserve male copulatory spicules. The buccal cavity of this free-living 'roundworm' is equipped with strong mandibles with hooked tips. This architecture clearly links *Palaeoenoploides* n. gen. to the enoplid nematode clade and suggests predatory/omnivorous feeding habits.

Key words: Enoplida, Cenomanian, Lebanon.

Riassunto - *Palaeoenoploides alessandrellianus* n. gen. n. sp.: un nematode tardo-Cenomaniano del Cretacico Superiore del Libano (Nematoda: Enoplidae).

Sulla base di 172 esemplari esaminati, viene di seguito descritto *Palaeoenoploides alessandrellianus* n. gen. n. sp., nematode a vita libera rinvenuto nei calcari sub-litografici cenomaniani di Haqel (Libano). Per la prima volta sono descritte le mandibole di un nematode fossile. Eccezionalmente, alcuni esemplari conservano traccia delle spicole copulatorie maschili. La cavità orale di *Palaeoenoploides* n. gen. è armata di solide mandibole a punta uncinata che indicano una relazione con la linea evolutiva degli enoplidi e un'alimentazione basata su attività predatoria.

Parole chiave: Enoplida, Cenomaniano, Libano.

Introduction

In recent years, marvelous examples of the preservation of invertebrates linked to groups sharing a poorly known evolutionary history due to their rather reduced fossil record have been recovered from the late Cenomanian *Lagerstätten* of Haqel (Lebanon). Such finds include exceptionally preserved annelid polychaetes (Alessandrello & Teruzzi, 1986; Bracchi & Alessandrello, 2005) and coleoid cephalopods (Fuchs, 2006; Fuchs *et al.*, in press): despite the nature of their body structure which mainly consists of non-mineralized tissues, these metazoans as well as the nematodes are relatively common in the Lebanese *Lagerstätten* and are usually well-preserved.

Approximately 20.000 living species assigned to the Phylum Nematoda which are commonly known as 'roundworms' due to the typical shape of the transversal section of their worm-like body. They represent one of the most successful invertebrate groups especially thanks to their small size and ecological adaptability. A number of species ranging between some hundred thousands and several millions is estimated for an enormous range of habitats and a fascinating array of lifestyles (Chitwood & Chitwood, 1974). The nematodes are common parasites infecting invertebrates (nematodes included), vertebrates (humans included) and plants and have a strong impact on their host populations (Théodoridès, 1965). The free-living forms inhabit almost every conceivable environment: soil, fluvial and lacustrine freshwater sediments, saltwater benthic habitats from the littoral zone to the deep sea and even pitcher plant and bromeliad aquatic leaf interstices, hot springs, alpine meadows, terrestrial glacial contexts, lacunary spaces of Arctic ice flows, damp plant litters, narrow stripes of detritus on trees, lichens and in rocky ranges (Goodey, 1963; Nicholas, 1975; Prejs, 1977; Tchesunov & Riemann, 1995; Andrásy, 1998; Holovachov, 2006).

The fossil nematodes are mostly known from Tertiary ambers that commonly preserve parasitic forms often hosting insects and sometimes free-living terrestrial forms (Poinar, 2003). Otherwise, the preservation of free-living aquatic nematodes in sedimentary rocks is rather rare so that they are often completely neglected in the invertebrate palaeontology treatises and fossil record monographs (Howell, 1962; Benton, 1992). At present, the fossil record of the free-living nematodes includes taxa from both terrestrial (von Duisberg, 1862; Menge, 1866; Taylor, 1935; Dollfus, 1950; Howell, 1962; Poinar, 1977; Manum *et al.*, 1994) and marine (Schram, 1973, 1979; Arduini *et al.*, 1983) palaeoenvironments. Similarly to *Palaeoenoploides alessandrellianus* n. gen. n. sp., both *Nemavermes mackeei* Schram, 1973 from the Pennsylvanian (Upper Carboniferous) of Mazon Creek (Illinois) and from the Mississippian (Lower Carboniferous) of Bear Gulch (Montana) and *Eophasma jurasicum* Arduini, Pinna & Teruzzi, 1983 from the Sinemurian (Lower Jurassic) of Osteno (Italy) were benthic marine organisms.

The terrestrial forms believed to be free-living are *Captivonema cretacea* Manum, Bose, Sayer & Boström, 1994 from the Barremian (Lower Cretaceous) of Spitsbergen (Svalbard Archipelago, Norway), entrapped in the viscous secretion of a clitellate cocoon and interpreted as having free-living habits in damp plant litter, and the microbotrophic plectid *Oligoplectus succinii* (von Duisberg, 1862) from the Lower Oligocene of Baltic Sea amber as well as the mermithids (Menge, 1866; Taylor, 1935) *Vetus capillacea* (Menge, 1866), *Vetus pristimus* (Menge, 1866) and *Vetus duisbergi* Taylor, 1935. Amber from Mexico also provided evidence of free-living terrestrial nematodes from the Upper Oligocene with the possible rhabditid *Vetus robustus* Poinar, 1977 and the diplogasterid *Oligodiplogaster antiquus* Poinar, 1977.

Finally, free-living nematode tracks dubitatively related to the extant dorylaimid genus *Dorylaimus* Dujardin, 1845 have been recorded in the Middle Eocene Green River Formation in Utah (Moussa, 1969).

Parasite nematodes often occur in amber with records extending back over 130 million years. Most of the latter have been found in association with insects and arachnids in the Lower Cretaceous of Lebanon and in the Paleogene of Dominican Republic, Baltic Sea and Mexico (Poinar, 2003). Vertebrate parasites have been found in the gut of ice-fossilized rodents (Dubinin, 1948; Rausch, 1957) and horses

(Dubinina, 1972) from the Pleistocene of Siberia, in Inca (Pizzi & Schenone, 1955) and Egyptian (Reyman *et al.*, 1976) human mummies and in a precolombian human coprolite (Dunn & Watkins, 1970) even if these latter discoveries actually lie outside the scope of palaeontology.

Finally, Poinar *et al.* (2008) recently provided the earliest evidence of an association between terrestrial plants and animals through the description of the Devonian enoplid nematode *Palaeonema phyticum* Poinar, Kerp & Hass, 2008.

Materials and methods

All of the 172 examined specimens (Tab. 1) come from Haqel (Lebanon) and they are held in the Palaeontological Collection of the Museo di Storia Naturale di Milano (MSNM). All the specimens are dorso-ventrally or laterally compressed and flattened on a two-dimensional surface of yellow-greyish limestone. Some specimens underwent both a dorso-ventral and a lateral compression due to the typically 'curled' posture of the nematode body. Both part and counterpart are preserved only in 21 specimens (Tab. 1). In some cases, several nematodes, annelid polychaetes, decapod crustaceans and/or fishes are preserved on the same slab. A SEM analysis has been carried out on the teeth of specimens MSNM i26242ab and MSNM i24941.

Tab. 1 - List of the examined MSNM specimens. (● = presence of organic matter inside the gut; ♂ = presence of male copulatory spicules; ab = part and counterpart available; roman numbers = specimens preserved on the same slab).

Tab. 1 - Elenco degli esemplari MSNM esaminati. (● = presenza di materiale organico all'interno del canale alimentare; ♂ = presenza di spicole copulatorie maschili; ab = impronta e controimpronta disponibili; numeri romani = esemplari diversi su una stessa lastra).

i8337	i16283XIII	i20561abI ♂	i23432II	i24925III ♂
i8471 ●	i16285I	i20561abII	i23433I	i24932
i8477	i16285II	i20561abIII ● ♂	i23433II ●	i24934I ●
i8484 ●	i16285III	i20561IV	i23433III ●	i24934II
i8485 ♂	i16285IV	i20561V	i23433IV	i24941
i8486I	i16285V	i20594I	i23433V	i24942
i8486II ●	i16285VI ●	i20594II	i23433VI	i24947
i9181 ●	i16285VIII	i20596	i23433VII	i24948
i9191	i16285IX	i20602	i23438	i24949I
i9205 ●	i16286I	i20604	i23444 ●	i24949II
i9361	i16286II	i20605	i23445 ♂	i24949III ●
i9368 ●	i16286III	i20606I ♂	i23446I	i24950 ●
i10764I ● ♂	i16286IV	i20606II	i23446II	i24968 ●
i10764II	i16286V	i20607	i23446III	i24969II
i12399	i16289 ●	i20622I	i23449 ●	i24969III ♂

i13285 ♂	i16290I	i20622II	i23451	i24971I
i13310	i16290II	i20622III ♂	i23456	i24971II
i16273 ● ♂	i16290III	i20626I ● ♂	i23459 ●	i24979 ♂
i16277	i16290IV ● ♂	i20626II	i23460I ●	i24987
i16280I	i16290V	i20631I ●	i23460II ●	i24995
i16280II	i16290VI	i20631II	i24908abI ♂	i24996
i16281I ● ♂	i16292	i20634	i24908abII	i24998 ●
i16281II ●	i16297	i20635	i24908abIV	i25010 ●
i16281III ●	i16301I	i20655I	i24908III	i25016ab
i16283I	i16301II ●	i20655II	i24908V	i26239I
i16283II	i16302I ●	i20655III	i24908VI	i26239II
i16283abIII ●	i16302II	i22834I	i24908VII	i26239III
i16283abIV	i16302III	i22834II	i24908VIII	i26240
i16283abV	i16301IV	i23050	i24908IX	i26241 ●
i16283VI	i18280	i23055	i24909 ♂	i26242ab ●
i16283abVII ●	i20560abI	i23481I	i24912	i26243ab
i16283abVIII	i20560abII ●	i23481II	i24923	i26244 ●
i16283abIX ♂	i20560abIII ● ♂	i23423	i24924	
i16283abX	i20560abIV ●	i23431	i24925I ●	
i16283XI	i20560abV	i23432I ●	i24925II	

The preserved soft parts include body outline together with gut outline and walls and are always evident as brownish imprints. However, setae and amphids as well as other organs, structures and ornamentations which usually bearing significant diagnostic features in modern nematode systematics are never evident.

The preserved sclerotized parts include the teeth and the male copulatory spicules. Sometimes (MSNM i12399, MSNM i16301), the teeth are evident as isolated clusters and lack traces of any other component of the organism. They are preserved as a black and shiny material very similar to that already described by Bracchi & Alessandrello (2005) for the teeth and chaetae of some annelid polychaetes from the same Lebanese outcrops. Actually, both the nematode and polychaete teeth are composed of sclerotized proteins that make them resistant against degradation. However, the polychaete scolecodonts are relatively common in the sedimentary rocks (Szaniawski, 1996) while nematode scolecodonts have never been observed prior to this study. This may be due both to the nature of the tiny and fragile nematode teeth and to the fact that isolate nematode mandibles could be misinterpreted, neglected or simply not observed.

Study area

The examined specimens come from the Late Cretaceous sub-lithographical limestones of Haqel in north-western Lebanon. Additional stratigraphic data are not available for the slabs examined in this study. Haqel is approximately 45 kilometres from Beirut and 12 km from the coastal city of Jbail (Byblos).

According to Hückel (1970), von Hemleben (1977) and Capetta (1980), the limestones from Haqel are hard, fine grained, well-bedded and laminated, often characterized by a rich fossiliferous content and by a yellowish colour that sometimes may become greyish. Some levels of the Haqel outcrop are particularly rich in flint nodules.

Recently, Wippich & Lehmann (2004) have confirmed a Late Cenomanian age for the Haqel limestones on the basis of the presence of the ammonite *Allocrioceras* cf. *annulatum*. *Allocrioceras* cf. *annulatum* is known from the Lower Upper Cenomanian *Sciponoceras gracile* Zone in the Western Interior of the U.S.A. and from the *Metoicoceras geslinianum* Zone in the International Standard Zonation Scheme.

During the Cenomanian, Lebanon and the whole Arabian peninsula were part of the African platform in the northern part of the Gondwana supercontinent (Philip *et al.*, 1993). Similarly to the Late Cenomanian Al-Namoura deposit (Dalla Vecchia *et al.*, 2002; Dalla Vecchia & Chiappe, 2004), the Haqel *Lagerstätte* reasonably formed in small and shallow Tethyan basins with a reduced water circulation, within a carbonate platform setting that covered parts of the Arabian craton between Albian and Turonian times. Within this scenario, mild oscillations of the relative sea level produced an exceptional sandwich of shallow water carbonate facies (Ferry *et al.*, 2007). The described palaeoenvironment produced favourable conditions of preservation of the palaeofauna which includes remnants of terrestrial plants together with a rich ichthyofauna, decapod and stomatopod crustaceans, annelid polychaetes, ammonoid and coleoid cephalopods and others (Bracchi & Alessandrello, 2005; Fuchs, 2006; Fuchs *et al.*, in press).

Systematic Palaeontology

Phylum Nematoda (Rudolphi, 1808)

Class Adenophorea (von Linstow, 1905)

Subclass Enoplia Pearse, 1942

Order Enoplida Schuurmans Stekhoven & de Coninck, 1933

Suborder Enoplina Chitwood & Chitwood, 1937

Superfamily Enoploidea (Schuurmans Stekhoven & de Coninck, 1933)

Family Enoplidae Baird, 1853

Subfamily Enoploidinae de Coninck, 1965

Genus *Palaeoenoploides* n. gen.

Diagnosis: as the type species.

Derivatio nominis: from the Greek *παλαιός* (= ancient) and from *Enoploides* Saveljev, 1912, the type genus of the subfamily Enoploidinae due to the strong similarity in the tooth apparatus arrangement.

Type species: *Palaeoenoploides alessandrellianus* n. sp.

Palaeoenoploides alessandrellianus n. sp.

Figs. 1-6

Diagnosis: powerful tooth apparatus formed of three hooked mandibles. Dorsal mandible doubly hooked, ventral mandibles with a single hook and two wand-like apophysis.

Derivatio nominis: dedicated to Anna Alessandrello, for her indispensable contribution to the knowledge of worm-like fossil metazoans.

Holotype: MSNM i13285 (Fig. 1).

Paratype: MSNM i26242ab (part and counterpart; Fig. 2), MSNM i24941 (Fig. 3), MSNM i24908abI (part and counterpart, Fig. 6).

Type locality: Haqel, Lebanon.



Fig. 1 - *P. alessandrellianus* n. gen. n. sp.: holotype/olotipo MSNM i13285 (body x 45; teeth x 435).

Type horizon: Metoicoceras geslinianum Zone of the International Standard Zonation Scheme (corresponds to the *Sciponoceras gracile* Zone in the Western Interior of U. S. A.). Lower Upper Cenomanian.

Material: 172 specimens (Tab.1).

Measurements: maximum length and width of holotype and paratypes together with the length and width maximum and minimum values of all the examined specimens and the average maximum length and width values of the whole examined collection are reported in Tab. 2.

Tab. 2 - Length and width measurements of the 172 examined specimens of *P. alessandrellianus* n. gen. n. sp. / Valori di lunghezza e larghezza dei 172 esemplari esaminati di *P. alessandrellianus* n. gen. n. sp.

Specimen	Length (mm)	Width (mm)
MSNM i13285 holotype	32	1.9
MSNM i24908abI paratype	26	0.9
MSNM i24941 paratype	24	1.1
MSNM i26242ab paratype	23	1.3
Whole Examined Collection	Length (mm)	Width (mm)
Average value	19	0.9
Maximum value	46	2.3
Minimum value	8	0.3

The average values of the maximum length and width of the dorsal and ventral teeth are reported in Tab. 3 (see also Figs. 2, 3).

Tab. 3 - Length and width measurements of the dorsal and ventral teeth of *P. alessandrellianus* n. gen. n. sp.

Tab. 3 - Valori di lunghezza e larghezza dei denti dorsale e ventrali di *P. alessandrellianus* n. gen. n. sp.

Teeth	Length (µm)	Width (µm)
Dorsal tooth	610	270
Ventral teeth	1120	200
Apophysis of the ventral teeth	460	35

Description: the body is worm-like and it essentially appears as a tube (the gut) within a tube (the body wall) so that in life *P. alessandrellianus* n. gen. n. sp. should show a cylindrical and slightly elongate shape.

As results from Tab. 2, the holotype maximum length is 32 mm, the maximum width measures 1.9 mm in the fore region. The width is generally constant along the whole body with the exception of a gradual reduction in the tail region. Behind the buccal cavity, a swelling probably coinciding with the aesophageal area is usually evident.

The cephalic extremity looks trenched and continuous with the rest of the body. It is usually easy to recognize it due to the presence of teeth.

The tooth apparatus apparently seems to be made up of eight elements measuring between 0.7 and 0.8 mm in length (Fig. 3). Four of them can be described as large sickle-shaped elements and the others as small wand-like elements. However, in most of the examined specimens, the artifacts of fossilization evidently produced the disarticulation of these elements thus rendering the true relations among the eight cited pieces. This is particularly evident in the specimens MSNM i8471, MSNM i16285II, MSNM i16285IV, MSNM i16290III, MSNM i16290IV, MSNM i16297, MSNM i20602, MSNM i20604, MSNM i23432I, MSNM i23433, MSNM i23445, MSNM i24941 (Fig. 2), MSNM i24948, MSNM i24949, MSNM i24979, MSNM i24998 and MSNM i25010.

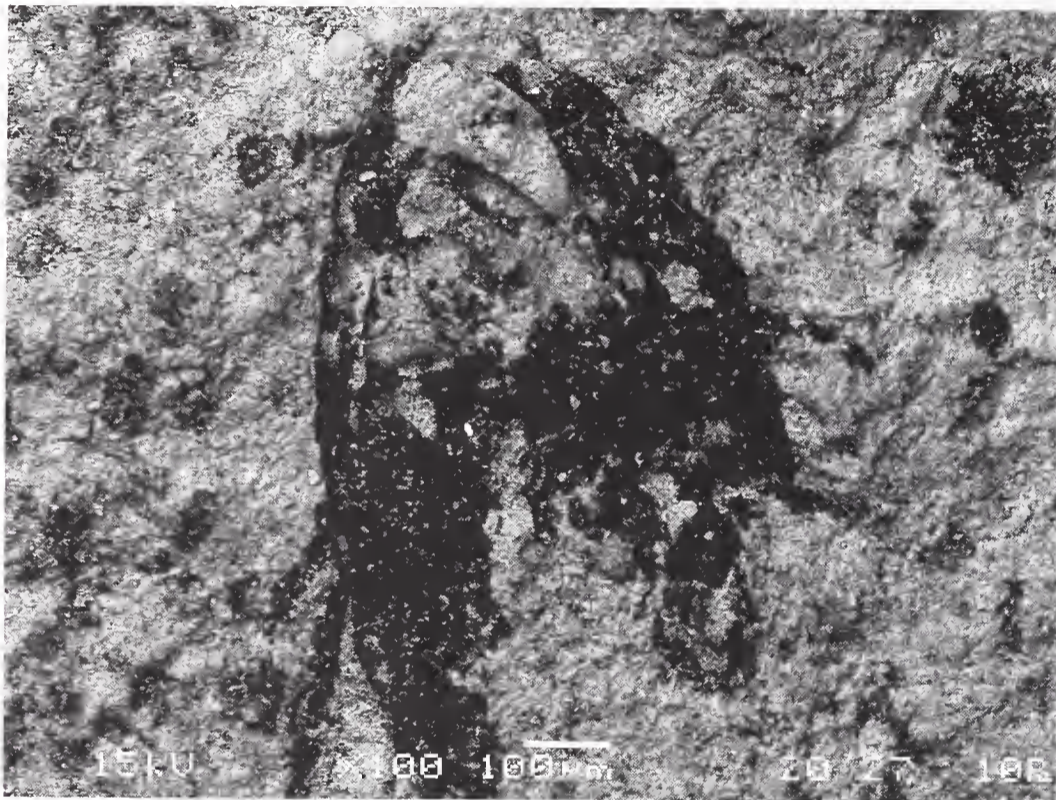


Fig. 2 - *P. alessandrellianus* n. gen. n. sp.: teeth of the paratype / denti del paratipo MSNM i26242ab (SEM photo by A. Guastoni).

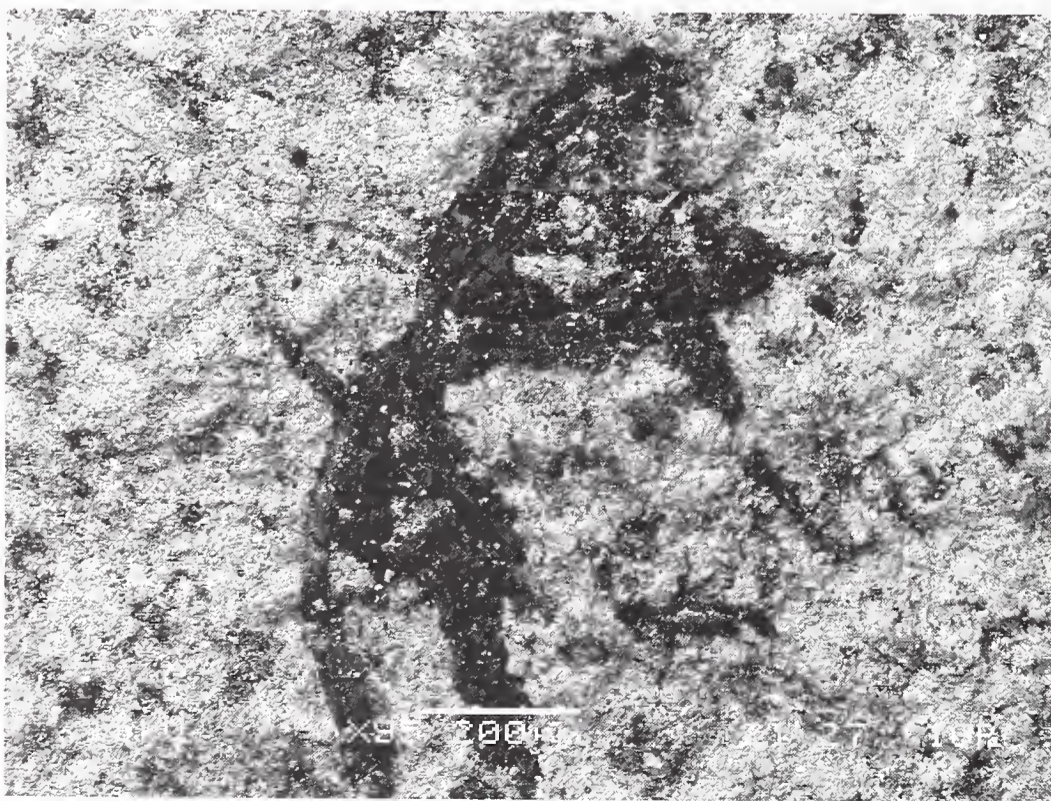


Fig. 3 - *P. alessandrellianus* n. gen. n. sp.: teeth of the paratype / denti del paratipo MSNM i24941 (SEM photo by A. Guastoni).

These samples share a similar preservation of the tooth apparatus showing eight elements organized in an X-shaped arrangement (Fig. 3) that hardly fits with the apparatus reconstruction herein proposed and with the general architecture of the free-living nematode apparatuses. In the opinion of the authors, the specimens that show such preservation of the tooth apparatus underwent a particular squeezing and twisting of the body that produced a compression of the head and a complete disarticulation of the teeth and their apophysis.

In the tooth apparatus reconstruction here hypothesized, the four wand-like elements can be interpreted as the basal bifurcations of two mandibles as clearly appears in some examined specimens (MSNM i9191, MSNM i16277, MSNM i16283IV, MSNM i16283VIII, MSNM i16285VI, MSNM i16290II, MSNM i16301I, MSNM i20560II, MSNM i20596, MSNM i20626II, MSNM i23433V, MSNM i23446III, MSNM i24932, MSNM i24934I). Analogous basal bifurcations has been described by de Coninck (1965) for the enoplid nematode mandibles of the Subfamily Enoploidinae. On the other hand, the four sickle-shaped elements sensibly represent the principal body of the three mandibles. Consequently, in the opinion of the authors, it appears evident that *Palaeoenoploides* n. gen. possessed a dorsal mandible with a doubly hooked body corresponding to two sickle-shaped elements without basal bifurcations and two ventral singly hooked mandibles each one corresponding to a sickle-shaped element bearing a basal bifurcation produced by two wand-like elements. The specimens MSNM i8484, MSNM i9361, MSNM i16277, MSNM i16285VI, MSNM i24925I, MSNM i24925III are those that better testify the proposed reconstruction of the tooth apparatus (Fig. 4, 5). The hooked tips of the mandibles are evidently turned toward the mouth opening in order to be useful in catching food.

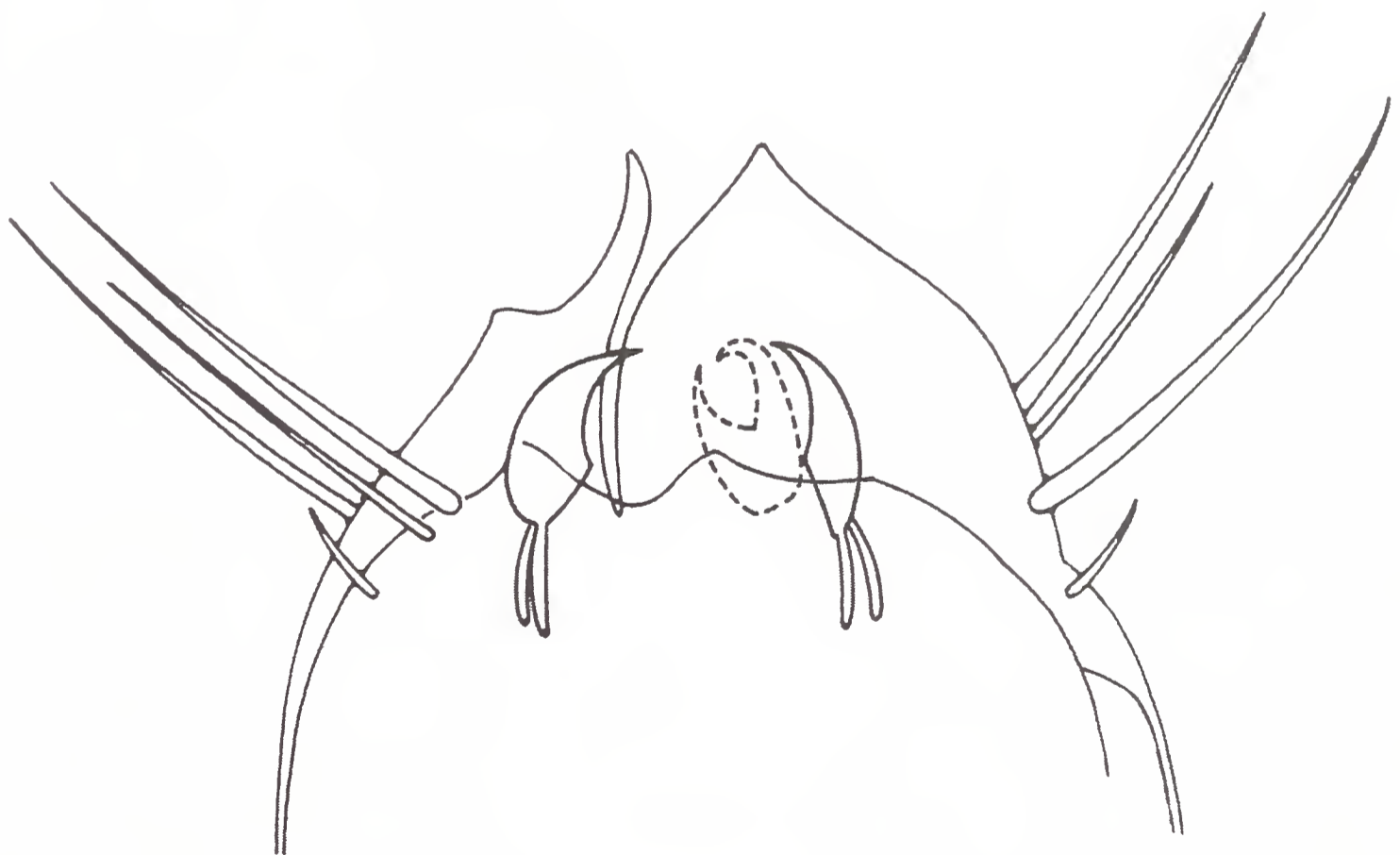


Fig. 4 - *P. alessandrellianus* n. gen. n. sp. (ventral view), reconstruction of the tooth apparatus. Body outline of an hypothetic enoplid nematode (line drawing by M. Demma).

Fig. 4 - *P. alessandrellianus* n. gen. n. sp. (norma ventrale), ricostruzione della dentatura. Contorno del corpo di un nematode enoplide ipotetico (disegno di M. Demma).

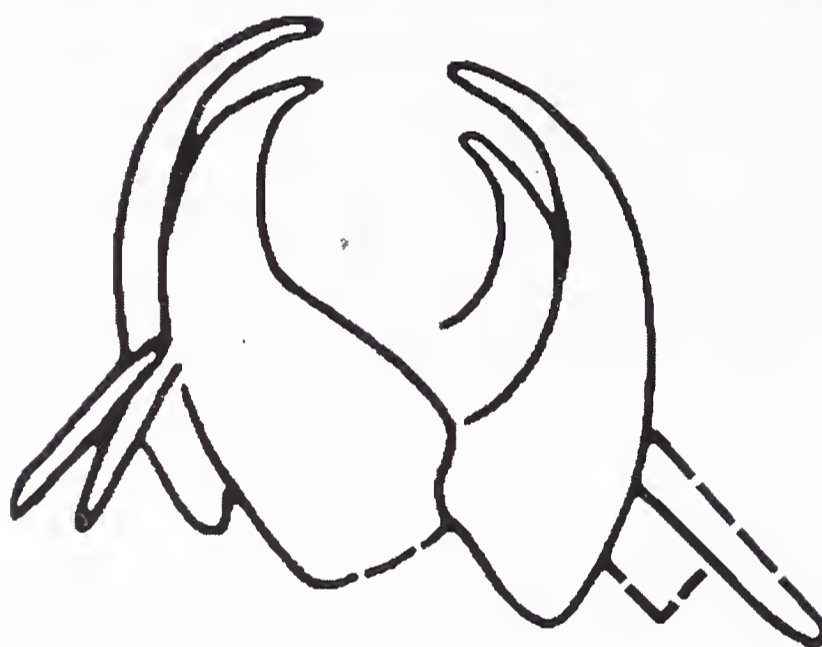
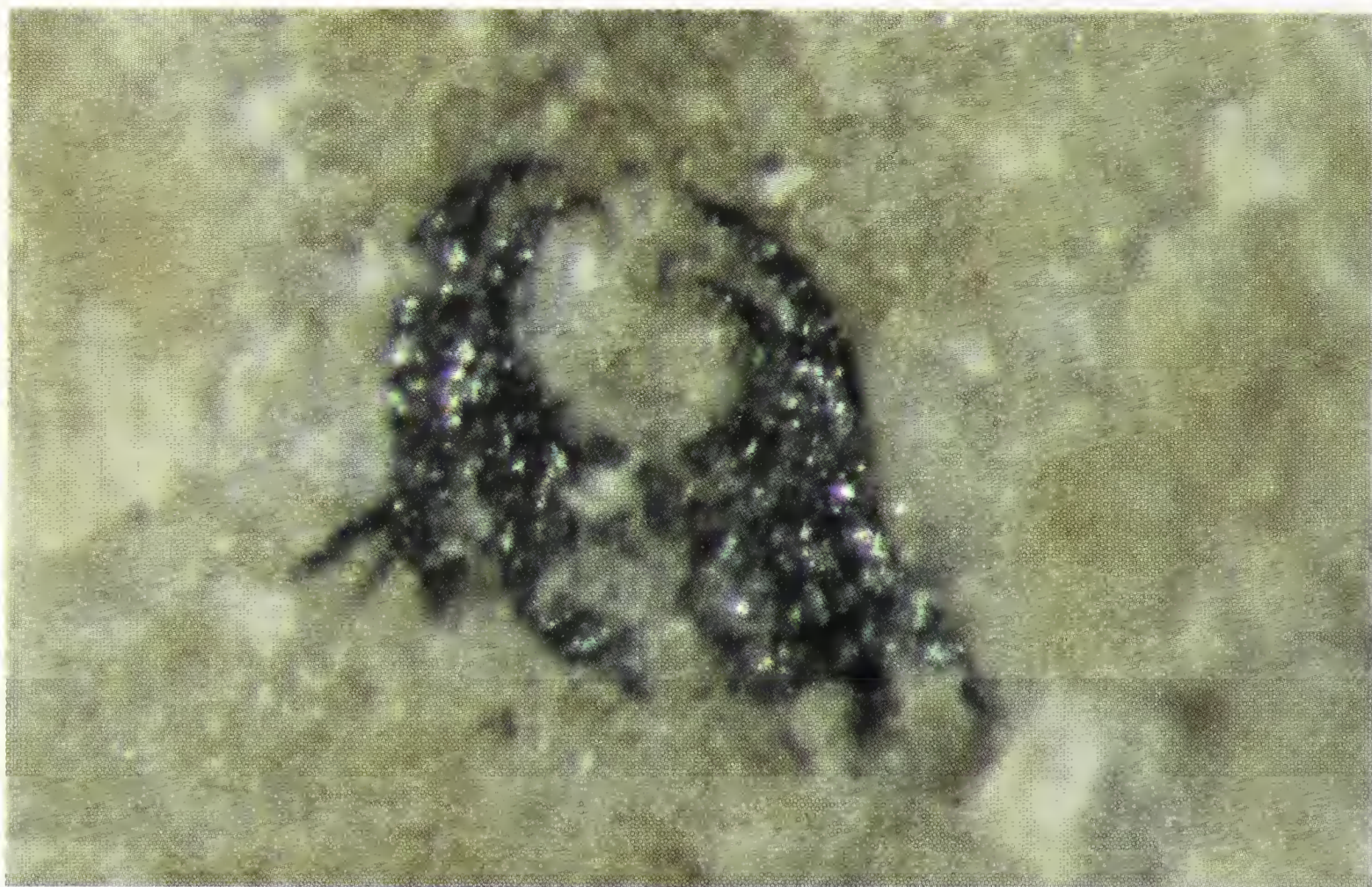


Fig. 5 - *P. alessandrellianus* n. gen. n. sp.: photo and line drawing of the teeth of / foto e disegno al tratto dei denti di MSNM i16285VI (x 325).

Near the caudal extremity of 18 specimens (Tab. 2), the copulatory spicules (male sclerotized reproductive organs) are preserved as tiny and thin rod-like structures. Due to their poor preservation, it is always impossible to define their exact number even if in modern adult males the reproductive system is generally composed of three elements (2 spicules and a *gubernaculum*).

In the paratype MSNM i24908abI, at a point three quarters along the length of the body, the wall of the gut is clearly evident as a double dark track parallel to the body outline (Fig. 6). Along the body of several specimens (Tab. 2) a darker colour area is evident inside the gut: it probably represents the remains of ingested food. This material is visible in different portions of the alimentary canal, generally behind the cephalic extremity close to the proximal intestine, sometimes closer to the tail.

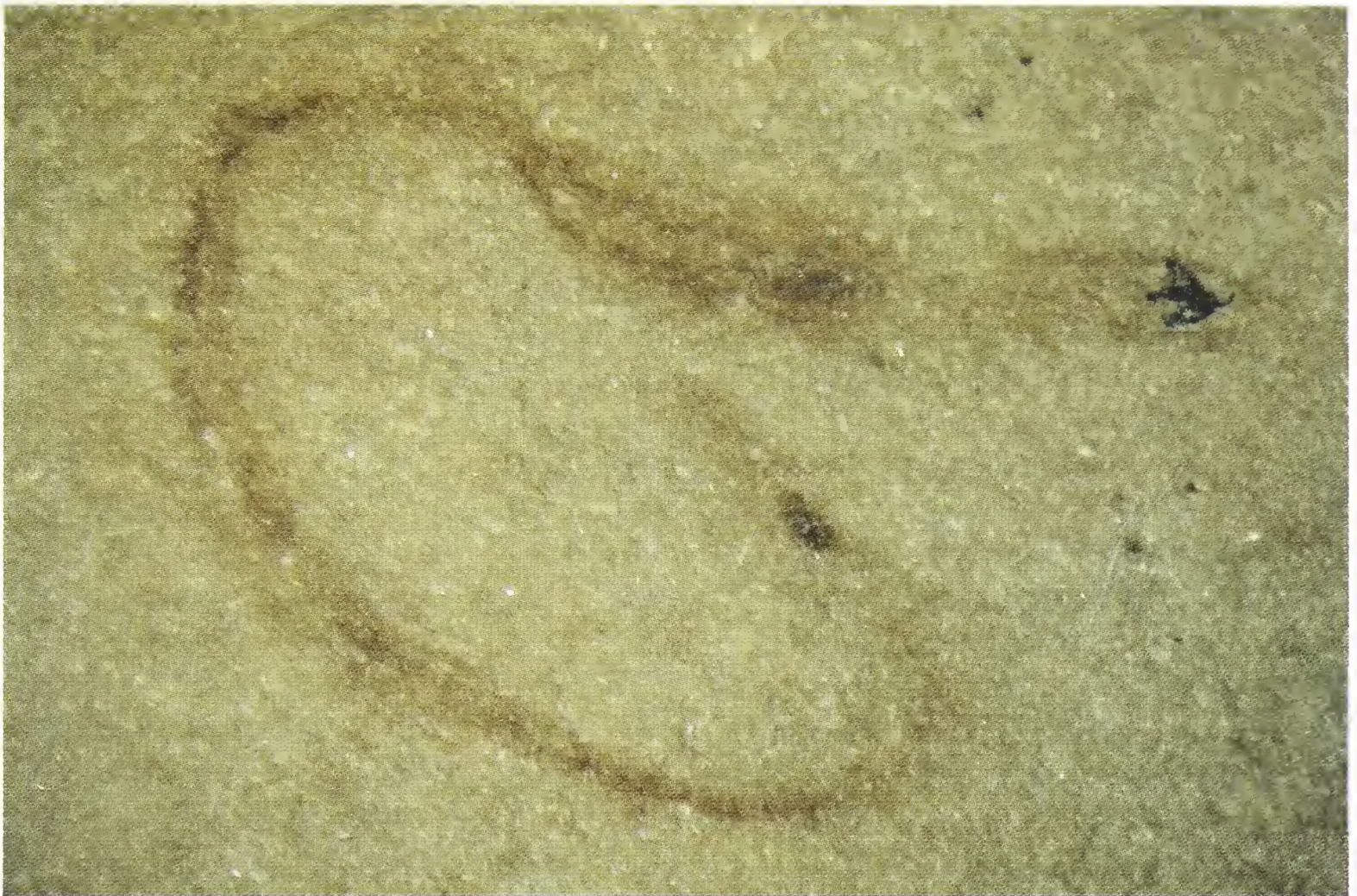


Fig. 6 - *P. alessandrellianus* n. gen. n. sp.: paratype / paratipo MSNM i24908abl (x 63).

Discussion

Morphological, taxonomical and phylogenetical remarks

The cylindrical shape of the body lacking deambulatory structures such as those observed in the annelid polychaete chaetae, the typical 'curled' posture of the body of the studied specimens and the architecture pattern of the mandibles together with the presence of male copulatory spicules clearly indicates that *Palaeoenoploides* n. gen. belongs to the Phylum Nematoda. Furthermore, the architecture of the buccal apparatus and the large size suggest a taxonomic position close to the enoplid nematodes of the Order Enoplida, Subclass Enoplia, Class Adenophorea. Large-size free-living nematodes sometimes possessing three powerful hooked teeth which morphologically are very close to those of *Palaeoenoploides* n. gen., in particular belong to the Family Enoplidae. Other groups of free-living Adenophorea such as those included in the Subclass Chromadoria (de Coninck, 1965; Platt & Warwick, 1983b) own an oral armour different in dimension, morphology and number of elements (one dorsal tooth and a set of denticles). Moreover, the morphology of the mandibles of *Palaeoenoploides* n. gen. closely resembles that of the modern genera included in the Subfamily Enoploidinae: *Enoploides* Saveljev, 1912, *Enoplonema* Kreis, 1934, *Hylacanthion* Wieser, 1959, *Lyranema* Timm, 1961, *Mesacanthoides* Wieser, 1953, *Metenoploides* Wieser, 1953 and *Parenoplus* Filipjev, 1927 (de Coninck, 1965; Platt & Warwick, 1983a). This similarity is particularly evident when the hooked tips of both the ventral and dorsal teeth as well as the presence of basal bifurcations in the ventral teeth are taken into consideration. Otherwise, the function of the wand-like elements is not so clear: perhaps, as Maggenti (1981) reports for some modern forms, they could have been apophyses supporting the oral muscles that probably allowed *Palaeoenoploides* n. gen. to evert the mandibles.

Actually, the Subfamily Enoploidinae represents, together with the genus *Enoplus* Bastian, 1865 of the Subfamily Enoplinae Filipjev, 1916, a pool of primitive enoplids possessing stout and hooked mandibles, ancestors of the other members of the Family Enoplidae through a gradual reduction of the teeth that have been involved in a structural hollowing and boring (de Coninck, 1965). Moreover, the presence in the Lebanese Late Cretaceous limestones of a enoplid nematode with well-developed and powerful mandibles very similar to those of the living representatives of the primitive Subfamily Enoploidinae seems to support the hypothesis considering the clade of Enoplida to have arisen between Silurian and Devonian (Poinar, 1983).

Comparing the Haqel nematodes with the other known free-living nematodes from marine palaeoenvironments *Nemavermes mackeei* and *Eophasma jurasicum*, no relationships can be pointed out. Actually, the absence of mandibles in both *N. mackeei* and *E. jurasicum* renders impossible an adequate comparison of the three species.

Reproduction

Eighteen studied specimens (Tab. 2) show structures recognizable as copulatory spicules near the caudal extremity. In modern male nematodes, the development of spicules is related to the reproductive stage of the nematode life cycle (Nigon, 1965; Poinar, 1983) so that it is possible to recognize the adult individuals when they are present. The range in length (20-45 mm) of the specimens of *P. alessandrellianus* n. gen. n. sp. with evident spicules contributes in supporting the assumption reported above. However, the artifacts of fossilization do not obviously allow to state for sure if the specimens without spicules are juveniles or females.

Autoecology

In the same way as the modern marine free-living nematodes and as the mode of preservation suggests, *P. alessandrellianus* n. gen. n. sp. reasonably was a benthic worm crawling on the surface of the seafloor or within the upper centimetres of the sediment. Moreover, *P. alessandrellianus* n. gen. n. sp. probably was a predator and fed upon micro-organisms and/or algae as the modern free-living marine nematodes do (Sliter, 1971; Hunt, 1977; Poinar, 1983), even if it has not been possible to identify the origin of the organic matter present inside the gut of several specimens (Tab. 1, Fig. 6). The assumption just outlined above is suggested especially by the morphology of the mandibles, revealing that with their hooked tips turned toward the mouth opening and with their apophyses linked to the oral muscles they should have been evertable predatory structures for capturing and holding food (Jensen, 1987).

Some studies on the annellid polychaetes from the same outcrops of *P. alessandrellianus* n. gen. n. sp. (Bracchi & Alessandrello, 2005) gave evidence of the presence of a nematode buccal apparatus inside the alimentary canal of an undetermined polychaete from Haqel (MSNM i12402) indicating that some polychaetes predated upon nematodes as the extant ones do (Esser & Sobers, 1964). Moreover, two nematode specimens (MSNM i12399, MSNM i16301) preserved as small clusters of isolated teeth can be interpreted as the stomach flush or coprolites of different predators, such as fishes and crustaceans, both frequently associated to *P. alessandrellianus* n. gen. n. sp.

The meiofauna of modern marine and estuarine sediments is almost invariably dominated by nematodes. An enigmatic feature of modern marine nematode communities is their high species diversity: it is not uncommon to find from 50 to 800

species in 10 cm³ of sediment (Moens *et al.*, 1999). However, in this light, the relative abundance of a single nematode species in the Cenomanian sub-litographical limestones of Haqel appears even more enigmatic. Trotter & Webster (1984) demonstrated that 3 dominant nematode species are differentially attracted to several types of bacterial and microalgal food. Decaying organic matter has been shown to attract some nematode species and to repel others (Gerlach, 1977; Lorenzen *et al.*, 1987). Moreover, Moens *et al.* (1999) focused on the nematode spatial distribution and reduction of the nematode specific diversity to different strains of bacteria, to bacteria sampled from differently aged cultures, to different densities of bacteria, to bacterial growth medium and to substances released by the bacteria.

Acknowledgements

The authors wish to thank Anna Alessandrello and Giorgio Teruzzi (Museo di Storia Naturale di Milano), George Poinar Jr. (Oregon State University) and Aldo Zullini (Università degli Studi di Milano - Bicocca) for the useful advice and criticism, Massimo Demma for the line drawings, and Alessandro Guastoni for the SEM photographs. All the photos and drawings are by Alberto Mattavelli if not otherwise specified.

References

- Alessandrello A. & Teruzzi G., 1986 – *Eunicites phoenicius*, a new fossil polychaete anellid of the Cenomanian of Haqel, Lebanon. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano*, Milano, 127 (3-4): 321-325.
- Andrássy I., 1998 – Nematodes in the sixth continent. *Journal of Nematode Morphology and Systematics*, Jaén, 1: 107-186.
- Arduini P., Pinna G. & Teruzzi G., 1983 – *Eophasma jurasicum*, a new nematode of the Sinemurian of Osteno in Lombardy. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano*, Milano, 124 (1-2): 61-64.
- Benton M. J. (ed.), 1982 – The fossil record 2. *Chapman & Hall*, London.
- Bracchi G. & Alessandrello A., 2005 – Paleodiversity of the free-living polychaetes (Annelida, Polychaeta) and description of new taxa from the Upper Cretaceous *Lagerstätten* of Haqel, Hadjoula and Al-Nammoura (Lebanon). *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, Milano, 32 (3): 1-64.
- Capetta H., 1980 – Les Sèlaciens du Crétacé Supérieur du Liban. I. Requins. *Palaeontographica, Abteilung A, Paläozoologie-Stratigraphie*, Stuttgart, 168: 69-148.
- Chitwood B. G. & Chitwood M. B., 1974 – Introduction to nematology. *University Park Press*, Baltimore.
- Coninck de L., 1965 – Classe des nématodes. In: *Traité de Zoologie, Anatomie, Systématique, Biologie, Némathelminthes (Nématodes)*, Tome IV, Fasc. II. Grassé P. P. (ed.). *Masson et Cie Éditeurs*, Paris: 586-731.
- Dalla Vecchia F. M. & Chiappe L. M., 2002 – First avian skeleton from the Mesozoic of northern Gondwana. *Journal of Vertebrate Paleontology*, Norman, 22 (4): 856-860.

- Dalla Vecchia F. M., Venturini S. & Tentor M., 2002 – The Cenomanian (Late Cretaceous) Konservat-Lägerstätte in en-Nammoûra (Krsouâne Province), northern Lebanon. *Bollettino della Società Paleontologica Italiana*, Modena: 51-68.
- Dollfus R. P., 1950 – Liste des nemathelminthes connus a l'état fossile. *Compte Rendu Sommaire des Séances de la Société Géologique de France*, ser. 5, Paris, 20: 82-85.
- Dubin V. B., 1948 – Discovery of Pleistocene lice (Anoplura) and nematodes as a result of study of Indigirka ground squirrels. *Doklady Akademii Nauk SSSR*, Moskva, 62 (3): 417-420.
- Dubinina M. N., 1972 – A prehistoric nematode from a Pleistocene horse. *Parazitologiya*, St. Petersburg, 6: 441-443.
- Duisberg von H., 1862 – Beitrag zur Bernstein-Fauna. *Schriften der Physikalisch-Ökonomischen Gesellschaft zu Königsberg in Preussen*, Königsberg, 3: 31-36.
- Dunn F. L. & Watkins R., 1970 – Parasitological examinations of prehistoric human coprolithes from Lovelock Cave, Nevada. In: *Archaeology and the prehistoric Great Basin lacustrine subsistence regime as seen from Lovelock Cave, Nevada*. Heizer R. F. & Napton L. K. (eds.). *Contributions of the University of California Archaeological Research Facility*, Berkeley, 10: 176-185.
- Esser R. P. & Sobers E. K., 1964 – Natural enemies of nematodes. *Proceedings of the Soil and Crop Science Society of Florida*, Hollywood, 24: 326-353.
- Ferry S., Merran Y., Grosheny D. & Mroueh M., 2007 – The Cretaceous of Lebanon in the Middle East (Levant) context. *Carnets de Géologie*, Memoir 2007/02, Abstract 08, Maintenon: 38-42.
- Fuchs D., 2006 – Morphology, taxonomy and diversity of vampyropod coleoids (Cephalopoda) from the Upper Cretaceous of Lebanon. *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, Milano, 34 (2): 1-28.
- Fuchs D., Bracchi G. & Weis R., in press – New records of octopods (Cephalopoda: Coleoidea) from the Late Cretaceous (Upper Cenomanian) of Hâkel and Hâdjoula, Lebanon. *Lethaia*, Oslo.
- Gerlach S. A., 1977 – Attraction to decaying organisms as a possible cause for patchy distribution of nematodes in a Bermuda beach. *Ophelia*, Helsingor, 16: 151-165.
- Goodey J. B., 1963 – Soil and freshwater nematodes. *Methuen & Co. Ltd.*, London.
- Hemleben von C., 1977 – Rote Tiden und die oberkretazischen Plattenkalke im Libanon. *Neues Jahrbuch für Geologie und Palaontologie, Monatshefte*, Stuttgart, 4: 239-255.
- Holovachov O., 2006 – Morphology and Systematics of the Order Plectida Malakhov, 1982 (Nematoda). Ph.D. Thesis. *Wageningen University and Research Centre, The Netherlands*, Wageningen.
- Howell B. F., 1962 – Worms. In: *Treatise on invertebrate paleontology*. Moore R. C. (ed.). *Geological Society of America and University of Kansas Press*, Lawrence: 144-177.
- Hüchel U., 1970 – Die Fischschiefer von Hâkel und Hâdjoula in der Oberkreide des Libanon. *Neues Jahrbuch für Geologie und Palaontologie, Abhandlungen*, Stuttgart, 135 (2): 113-149.
- Hunt D. J., 1977 – Observations on the feeding of *Ironus longicaudatus* (Enoplina: Ironidae). *Nematologica*, Leiden, 23: 478-479.

- Jensen P., 1987 – Feeding ecology of free-living aquatic nematodes. *Marine Ecology Progress Series*, Halstenbek, 35: 187-196.
- Lorenzen S., Prein M. & Valentin C., 1987 – Mass aggregations of the free-living marine nematode *Pontonema vulgare* (Oncholaimidae) in organically polluted fjords. *Marine Ecology Progress Series*, Halstenbek, 37: 27-34.
- Maggenti A. R., 1981 – General Nematology. *Springer-Verlag*, New York.
- Manum S. B., Bose M. N., Sayer R. T. & Boström S., 1994 – A nematode (*Captivonema cretacea* gen. et sp. n.) preserved in a clitellate cocoon wall from the Early Cretaceous. *Zoologica Scripta*, Stockholm, 23 (1): 27-31.
- Menge A., 1866 – Ueber ein Rhipidopteron und einige Helminthen im Bernstein. *Scripten der Naturforschenden Gesellschaft in Danzig*, Danzig, 1 (3): 1-8.
- Moens T., Verbeeck L., de Maeyer A., Swings J. & Vincx M., 1999 – Selective attraction of marine bacterivorous nematodes to their bacterial food. *Marine Ecology Progress Series*, Halstenbek, 176: 165-178.
- Moussa M. T., 1969 – Nematode fossil tracks of Eocene age from Utah. *Nematologica*, Leiden, 15: 376-380.
- Nicholas W. L., 1975 – The biology of free-living nematodes. *Clarendon Press*, Oxford.
- Philip J., Bellion Y., Babinot J. F., Tronchetti G., Fourcade E., Ricou L. E., Guiraud R., Bellion Y., Herbin J. P., Combes P. J., Cornee J. J. & Dercourt J., 1993 – Late Cenomanian (94 to 92 Ma). In: Atlas Tethys Palaeoenvironmental Maps. Dercourt J., Ricou L. E. & Vrielynck B. (eds.). *Commission de la Carte Geologique du Monde*, Paris.
- Nigon V., 1965 – Développement et reproduction des nématodes. In: *Traité de Zoologie, Anatomie, Systématique, Biologie, Némathelminthes (Nématodes)*, Tome IV, Fasc. II. Grassé P. P. (ed.). *Masson et Cie Éditeurs*, Paris: 218-386.
- Pizzi T. & Schenone, 1955 – Discovery of eggs of *Trichuris trichiura* in the intestines of an Inca archeological body. *Tropical Medicine and Hygiene News*, Bethesda, 4: 6-9.
- Platt H. M. & Warwick R. M., 1983a – Free-living marine nematodes, Part I. British Enoplids. *Cambridge University Press*, Cambridge.
- Platt H. M. & Warwick R. M., 1983b – Free-living marine nematodes. Part II. British Chromadorids. *Cambridge University Press*, Cambridge.
- Poinar G. O. Jr., 1977 – Fossil nematodes from Mexican amber. *Nematologica*, Leiden, 23: 232-238.
- Poinar G. O. Jr., 1983 – The natural history of nematodes. *Prentice-Hall Inc.*, Englewood Cliffs, New Jersey, U.S.A.
- Poinar G. O. Jr., 2003 – Trends in the evolution of insect parasitism by nematodes as inferred from fossil evidence. *Journal of Nematology*, Lawrence, 35 (2): 129-132.
- Poinar G. O. Jr., Kerp H. & Hass H., 2008 – *Palaeonema phyticum* gen. n., sp. n. (Nematoda: Palaeonematidae fam. n.), a Devonian nematode associated with early land plants. *Nematology*, Köln, Leiden, Boston, 10 (1): 9-16.
- Prejs K., 1977 – The littoral and profundal benthic nematodes of lakes with different trophy. *Ekologia Polska*, Warszawa, 25: 21-30.
- Rausch R., 1957 – Distribution and specificity of helminths in microtine rodents: evolutionary implications. *Evolution*, Lawrence, 11 (3): 361-368.
- Reyman T., Barroco A. & Cockburn A., 1976 – Histopathological examination of an Egyptian mummy. *Bulletin of the New York Academy of Medicine*, New York, 52: 506-516.

- Schram F. R., 1973 – Pseudocoelomates and a nemertine from Illinois Pennsylvanian. *Journal of Paleontology*, Tulsa, 47 (5): 985-989.
- Schram F. R., 1979 – Worms of Mississippian Bear Gulch Limestone of central Montana, U.S.A. *Transactions of the S. Diego Society of Natural History*, S. Diego, 19 (9): 107-120.
- Sliter W. V., 1971 – Predation on benthic foraminifers. *Journal of Foraminiferal Research*, Washington, 1: 20-29.
- Szaniawski H., 1996 – Scolecodonts. In: Palynology: principles and applications. Jansonius J. & McGregor (eds.). *American Association of Stratigraphic Palynologist Foundation*, Dallas: 337-354.
- Taylor A. L., 1935 – A review of the fossil nematodes. *Proceedings of the Helminthological Society of Washington*, Washington, 2 (1): 47-49.
- Tchesunov A. V. & Riemann F., 1995 – *Cryonema*. Arctic sea ice nematodes (Monhysteroidea), with descriptions of *Cryonema crassum* gen. n., sp. n. and *C. tenue* sp. n. *Nematologica*, Leiden, 41: 35-50.
- Théodoridès J., 1965 – Particularités physiologiques des nématodes. In : *Traité de Zoologie, Anatomie, Systématique, Biologie, Némathelminthes (Nématodes)*, Tome IV, Fasc. II. Grassé P. P. (ed.). *Masson et Cie Éditeurs*, Paris: 512-564.
- Trotter D. B. & Webster J. M., 1984 – Feeding preferences and seasonality of free-living marine nematodes inhabiting the kelp *Macrocystis integrifolia*. *Marine Ecology Progress Series*, Halstenbek, 14: 151-157.
- Wippich M. G. E. & Lehmann J., 2004 – *Allocrioceras* from the Cenomanian (mid-Cretaceous) of the Lebanon and its bearing on the palaeobiological interpretation of heteromorphic ammonites. *Palaeontology*, London, 47 (5): 1093.

Ricevuto: 27 febbraio 2008

Accettato: 16 aprile 2008